

visual perception to detect predators, and probably also to maintain contact with conspecifics, to develop the 'high-sit' as early as possible in order that they are able to elevate themselves and extend their visual field. On the other hand, the solitary genera such as *Atilax* and *Herpestes ichneumon* tend to occur in more densely vegetated habitats, where visual predator detection is less important due to availability of continuous cover. In the case of *Atilax* this cover is extended by virtue of its nocturnal habit.

Manipulation and breaking open of hen's eggs varies quite markedly, with dwarf mongooses and marsh mongooses developing the ability earliest. Because all the herpestines appear to favour eggs little ecological significance can be attributed to the time at which this pattern develops in the different species, and it is more likely to be related to physical ability. RASA (1973a) notes that young *Helogale* are particularly voracious and for such a small animal to manipulate objects clearly requires considerable motivation and dexterity. In relation to head-body length, limb length in *Galerella* is shorter even than that of *Helogale* and this may account for the much delayed development in this genus.

In all herpestines the rapid development of locomotory abilities is clearly adaptive, in that it allows young to accompany their parents on foraging trips as soon as weaning commences, thus reducing parental responsibility as far as provisioning the young are concerned.

Development of scent-marking behaviour shows some variation. The sociable species (*Mungos* and *Helogale*) exhibit earlier development of both anal and cheek-marking, than the solitary *Atilax*, although slight overlap in anal marking development occurs between *Atilax* and *Helogale*. In order to promote integration into a sociable group it would be expected that early development of scent-marking methods would occur. As the anal mark is the 'identity mark' of the individual (RASA 1973b; GORMAN 1976; HEFETZ et al. 1984), it is not surprising that it develops early in sociable mongooses, where identification of all group members is desirable. In *Helogale*, however, it develops after cheek marking, which might be related to the handstand position which is adopted during anal scent deposition. It seems that this would be a more difficult task to perform than the simple anal drag produced by *Mungos* and *Atilax*, and so develops when locomotion and balance are co-ordinated. In *Atilax* the cohesiveness of the rearing group is not well developed, and so the early development of anal marking is essential to reinforce the short-lived rearing bond.

Purring has been recorded for most herpestines (Tab. 3). PETERS (1984) considers that vocalizations with a uniform structural pattern consisting of a rhythmical series of short, low-intensity sounds constitute close range friendly communication (including purring). In *Atilax* the only sound that falls into this category is the "grizzle" (BAKER 1988).

Despite the marked differences in rearing systems between solitary and sociable herpestines, the similarities in the development of postnatal behaviour patterns illustrates the overall cohesiveness of the group and provides few clues concerning phylogeny.

Zusammenfassung

Beobachtungen über die postnatale Verhaltensentwicklung von Sumpfmangusten (Atilax paludinosus)

Die mütterliche Pflege bei Sumpfmangusten wird beschrieben. Sie besteht aus Säugen, Reizen zum Harnen, Schutz und Lehren aller Geschicklichkeiten. Der Beginn von neun verschiedenen Verhaltenskategorien wird kontrolliert und beschrieben. Diese schlossen Lautgebung, Bewegungen, Putzen, Schreck, Geruchsmarkierung, Spiel und sexuelles sowie agonistisches Verhalten ein. Im Vergleich mit der nachgeburtlichen Verhaltensentwicklung anderer Vertreter der Herpestinen, zeigten Sumpfmangusten gewisse Ähnlichkeiten.

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Author's address: CAROLYN M. BAKER, Zoology Department, University of Durban-Westville, PbX 54001, Durban, 4000, R. S. A.

Interpreting social behaviour of Wood bison using tail postures

By P. E. KOMERS, KATHRIN ROTH and RUTH ZIMMERLI

Department of Biology, University of Saskatchewan, Saskatoon, Saskatchewan, Canada

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Abstract

Free ranging wood bison were observed to investigate the use of tail postures during social interactions. Our observations support the following conclusions: 1. Different tail postures were exhibited in different social contexts. Tail wagging was associated with grazing, while holding the tail horizontally or up were associated with aggression, sexual behaviour, and danger. 2. When bulls and cows were found together in groups, mostly cows raised their tails when disturbed by predators, while bulls raised their tail in sexual contexts. 3. In aggressive interactions between bulls, tail up was associated with dominance, tail wagging with submission. 4. The tail up posture was exhibited in more intensive situations than the horizontal tail posture, suggesting that the tail up posture was a graded form of the tail horizontal posture. 5. Individuals involved in play fights did not raise their tails, while at least one of two contestants raised the tail at the end of (but not during) escalated fights. We conclude that the recording of tail postures of bison can serve as an objective tool in the interpretation of bison social behaviour. The role of the tail posture as a possible signal in bison communication is discussed.

Introduction

Understanding social behaviour of animals requires the knowledge of the behavioural repertoire employed by animals in social interactions. For this reason a detailed account of body postures has been given, for example, for wolves (*Canis lupus*) and domestic cats (*Felis catus*) (SCHENKEL 1947; LEYHAUSEN 1956). Tail postures in these species could be related to either dominance status, or state of emotions (level of fear or aggression). HAUSEFATER (1977) presented a quantitative analysis of tail postures in baboons (*Papio cynocephalus*), in which he showed that tail posture correlated with age but not rank. Some studies on ungulates describe tail postures in addition to descriptions of body postures (JARMAN 1979; BARRETTE 1977; CARO 1986).

Our observations of free-ranging wood bison (*Bison bison athabasca*) support the concern put forward by MCHUGH (1958) that bison behaviour patterns are often subtle and, therefore, difficult to determine objectively. Tail postures of bison have been often referred to in reports on bison social behaviour (MCHUGH 1958; FULLER 1960; EGERTON 1962; HERRIG and HAUGEN 1969; LOTT 1974; MAHAN 1978), suggesting that tail postures of bison might be indicative of either dominance status, level of aggression, or fear. In bison, strong development of hair on the head and neck region, and the large hump obscure objective descriptions of body postures such as the position of ears, stretching of the neck, and arching or stretching of the back. The tail, however, is a conspicuous body part and can be easily observed in relation to social behaviour.

In the above mentioned studies bison were observed to raise their tails to various degrees during aggressive, sexual, and alert behaviours, while they wagged their tails during grazing. However, no quantification or rigorous examinations of relationships were presented. Understanding the use of the tail in bison could be helpful in the interpretation of bison social behaviour. This paper describes the position of the tail of wood bison as a character feature in different social contexts.

Materials and methods

The study was conducted on a free-ranging wood bison population in the Mackenzie Bison Sanctuary (MBS), Northwest Territories, Canada. There are no human settlements in the MBS, only one road leads through the area, and no fences restrict the movements of bison. During the time of this study, the population size was estimated at 2500 wood bison. The area used by the bison was approximately 10 000 km² (GATES and LARTER 1990). The study was carried out from July 16 to August 16, 1990. The study area was Falaise Lake which was considered to be the core of the range of bison in the MBS (GATES and LARTER 1990). Falaise Lake extends over approximately 60 km². It is a shallow lake consisting largely of open sedge (*Carex* spp.) meadows and willow (*Salix* spp.) savannah. The lake is surrounded by boreal forest.

Bison groups are highly fluid and associations among individuals are considered near random (LOTT and MINTA 1983; VUREN 1983). Observations on individuals marked with radio transmitters suggest that individuals range widely, using most of the area in and around the MBS. It is our impression that a major part of the individuals in the population spent some time on the study area during the data collection for the present study, and that the events sampled largely represent different individuals.

For behavioral observations, the minimum number of bison observed was three. When we spotted bison groups at a distance (usually > 150 m), we left the all terrain vehicles behind and approached the animals by foot. By hiding in the vegetation, we made an effort not to be detected by the animals. Bison which detected humans generally left the area immediately. Therefore, we believe that the behavioral data collected during this study was not affected by the presence of observers.

Binoculars and telescopes were used to observe the animals. Each observational session lasted one to three hours. We left the site after this time interval, in order to search for a new group of bison. This method was chosen in an attempt to maximize the number of different individuals observed. Approximately 80 h of observation were conducted by each of the authors and one additional observer. In addition to recording behaviour in the field, a video camera with a 12 × lens was used to record bison behaviour on VHS video tape.

Categories of behaviour

Seven categories of behaviour were noted: walk towards another individual; walk away from another individual; walk with another individual (includes parallel and one behind another); standing (animal standing with its head up); grazing (animal standing or walking with mouth in grass); lying; and flehmen (HERRIG and HAUGEN 1969; LOTT 1974).

Tail postures

Four categories of tail posture were recorded (Fig.): tail wagging (tail hanging down and whipped to either side at least every ten seconds; McHUGH [1958] termed this posture "tail switching"); tail down (tail hanging down with no lateral movement); tail horizontal (proximal half of tail held horizontally; distal half of tail may or may not hang down); tail up (tail raised higher than 45° from horizontal). These tail postures were recorded when they were displayed for at least ten seconds. Transitory postures lasted less than ten seconds and were thus not recorded (for example, when lifting the tail from tail down to tail up, the tail was held for a brief moment at the horizontal position).

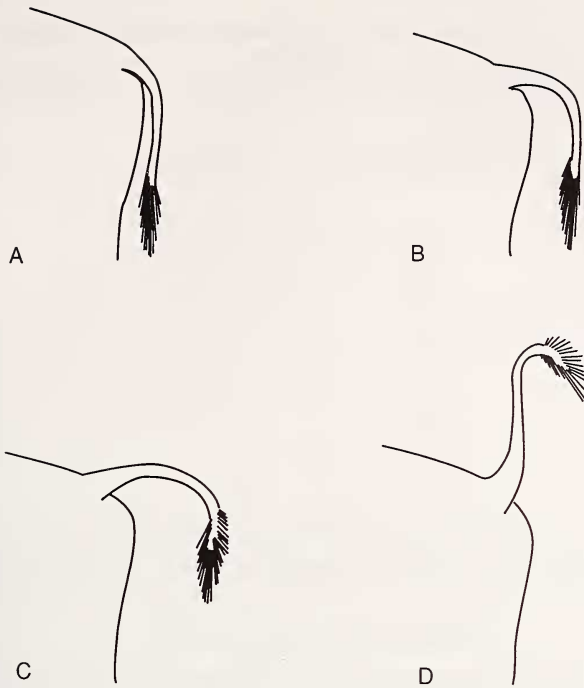
Context situations

Five context situations were recognized.

1. Grazing: The animal stood or walked with its head in the grass. Data on tail postures in the grazing context were collected from video tape. Each grazing animal was recorded on a data sheet once, when it and its tail posture could be first identified. Tape sequences were discarded, when there was a chance that individuals would be recorded a second time.

2. Alert: The animal stood with its head up and ears directed towards the source of danger. Bison groups disturbed by humans, were recorded on video tape. Each bison was recorded on a data sheet once, at the instant when it and its tail posture could be first identified. Because the different scenes of each group likely included the same individuals, the average frequency of bison adopting a given tail posture was calculated over the number of scenes. The averages from different groups were used as independent data points for statistical analysis.

3. Sexual context: A bull sniffed the genitals of a cow. Tail posture and category of behaviour were recorded for each of two interacting animals at the beginning and at the end of an interaction. An interaction started when one animal approached another to within two body lengths. This distance



Schematic representation of tail postures of wood bison. A: tail down; B and C: two forms of tail horizontal at the lower (B) and upper (C) margin of our definition (see text); D: tail up. Tail wagging was similar to tail down, except with lateral movements

was an arbitrary measure. The end was marked when one animal moved away from the other or when at least one animal changed its behaviour. Although some events were recorded in the same groups of bison, we assume that different individuals contributed to our observations. This assumption is based on the large number of individuals in groups, and the frequent changes of individuals between groups (KOMERS, unpubl. data). Tail postures of bison during sexual contexts were also recorded on video tape. For each interaction in which the bull showed tail up, his tail posture was also noted, by rewinding the tape, when he was more than two body lengths from the cow.

4. Aggression: An aggressive interaction was defined as one bull approaching another to within two body lengths and, subsequently, one of the two bulls turning away using at least two steps. The individual that turned away was considered the loser. This definition included subtle forms of interactions as well as escalated fights. Data were collected and analyzed in the same way as under "sexual context", except that instead of a cow, a bull was approached by another bull.

5. Locking horns: Two animals of any sex and age class standing head to head with horns touching when the interaction was first recorded. If an aggressive interaction resulted in a fight and, therefore, the two animals locked horns, the locking horn behaviour was considered part of an aggressive interaction and consequently not recorded under 5. Category 5 was established because some interactions were only noticed at the time when two animals locked horns.

When video tape recordings were used for data collection, the same criteria for behaviour and tail postures were applied, as for observations in the field. The tape was not played back in slow motion to make behaviours or tail postures more obvious.

Results

Tail postures in different contexts

On average, $97.3\% \pm 7.0\%$ (SD) of grazing animals were tail wagging. Of the 115 animals sampled, two held their tail horizontally, and four showed tail down. No animal was grazing with its tail up.

Table 1. Tail postures of wood bison displayed in different contexts at the start and at the end of an interaction

The numbers represent all animals involved, including both interacting partners

Tail Posture	Aggression	Behavioural context Locking horns	Sexual
Start			
Up	10	1	19
Horizontal	8	0	6
Down	7	0	11
Wagging	7	17	7
End			
Up	10	2	17
Horizontal	3	1	5
Down	4	1	12
Wagging	15	14	6

Tail posture varied in different context situations (Tab. 1: start of interactions, $\chi^2 = 40.4$, $df = 6$, $p < 0.001$; end of interactions: $\chi^2 = 24.8$, $df = 6$, $p < 0.001$). Both at the start and at the end of interactions, tail wagging was most often displayed in the locking horns context, while tail up was used more often in aggressive and sexual contexts (Tab. 1).

During alert behaviour, the average frequencies of the four tail postures observed were significantly different (up: 3.7; horizontal: 1.6; down: 3.2; wagging: 0.3; averaged over three groups with three video sequences each), indicating that tail up was observed most, and tail wagging least frequently (Kruskal-Wallis test with χ^2 -approximation, $\chi^2 = 8.08$, $df = 3$, $p = 0.044$).

Table 2. Tail postures of wood bison bulls and cows during sexual context

The numbers represent all animals involved, including both interacting partners

	Tail posture			
	Up	Horizontal	Down	Wagging
Bulls	16	2	0	3
Cows	1	3	12	4

In sexual contexts, bulls that sniffed the genitals of cows exhibited tail up most frequently, while females exhibited tail down most often (Tab. 2, Fisher exact, $p < 0.001$). Note that females exhibited tail down more often than tail wagging. Conceivably, tail wagging would interfere with the investigative behaviour of bulls.

Also in the sexual context, tail up was mostly associated with walk towards, while tail down and horizontal were associated with standing and grazing at the start of interactions (Tab. 3, Fisher exact, $p < 0.001$). At the end of interactions tail up was mostly associated with flehmen, while tail down and wagging mostly with standing and grazing (Tab. 3, Fisher exact, $p < 0.001$). Because sex probably influenced tail posture and behaviour, a two-way analysis of the contingency table would have been appropriate. However, small cell frequencies did not allow for such an analysis.

Tail posture as indicator of dominance

Only 6 of the 16 pairs of aggressively interacting bulls contained at least one of the contestants with a wagging tail at the start of the interaction, compared to 13 of 16 pairs at the end ($\chi^2 = 6.3$, $df = 1$, $n = 32$, $p = 0.012$). This suggests that one of the two bulls changed his tail posture to wagging during the interaction.

Independently of the above results, we recorded the winners, losers and the tail postures in 23 interactions for which the tail could be observed only at the end. Winners had their tails either up (21) or down (2), while losers had their tail either down (14) or

Table 3. Tail postures of wood bison at the start and at the end of sexual interactions

The numbers in parentheses represent tail postures for males only. The difference between the sample sizes at the start and end was because some tails were out of sight at the end of the interaction

Tail posture	Behavioural category		
Start			
	Walk towards	Stand	Graze
Up	19 (19)	0	0
Horizontal	2 (2)	3 (0)	1 (0)
Down	0	5 (0)	6 (0)
Wagging	1 (1)	5 (0)	1 (0)
End			
	Stand	Graze	Flehmen
Up	1 (0)	0	15 (15)
Horizontal	2 (0)	0	3 (3)
Down	7 (0)	5 (0)	0
Wagging	2 (1)	1 (1)	3 (3)

wagging (8) (Fisher exact, $p < 0.001$). Tail horizontal was not observed. This suggests that dominant bulls exhibit tail up, while submissive bulls exhibit tail wagging.

Tail as an indicator of intensity

We assumed that the distance between an actor and an interacting partner is equivalent to the intensity of a possible stimulus on the actor (MANNING 1979; Alcock 1989). If true, and if tail up reflects a stronger reaction than tail horizontal, then one would expect that animals further away from their interacting partners would exhibit tail horizontal more often than tail up. Alternatively, bulls that are aggressive could remain with tail up for extended periods of time, irrespective of the proximity of interacting partners.

Bulls were recorded with their tails up within two body lengths of a cow (sexual context) in nine video sequences. When they were further than two body lengths, either before or after approaching and sniffing, they showed tail horizontal in eight and tail up in one instances (binomial two-tailed test, $p = 0.02$).

Bulls were recorded with their tails up within two body lengths of a bull (aggressive context) in nine video sequences. When they were further than two body lengths, either before or after approaching, they showed tail horizontal in eight, and tail up in one instances (binomial two-tailed test, $p = 0.02$).

We conclude that the tail up posture was exhibited in more intensive situations than the tail horizontal posture. This response suggests that tail up was a graded form of tail horizontal.

Play fights and escalated fights

Nine fights among mature bulls were recorded on video tape. In all cases, bulls wagged their tail during the fight. In seven of the nine cases, one of the contestants exhibited tail up at the end of the fight. Thus, the tail was raised significantly more often at the end than during a fight (Fisher's exact, $df = 1$, $p = 0.002$). This observation suggests that in order to distinguish play fights (termed "play battles" by McHUGH 1958) from escalated fights, the position of the tail should be noted at the end of an interaction, and not while the animals lock horns.

This conclusion is further supported by results presented in Table 1. Both individuals exhibiting tail up under the locking horns context were mature bulls interacting with other mature bulls. The other individuals recorded in this context included three pairs of

subadult bulls, three pairs of yearlings, and one pair of calves. Presumably, immature bison fight for training their motor skills as opposed to competing for resources (ROTHSTEIN and GRISWOLD 1991). Indeed, in only one of the cases involving immature bison, interacting partners walked away from each other. The others either remained standing together or walked away together. In both cases in which one of the bulls raised his tail, the two contestants walked away from each other.

Discussion

When bison in our study did not interact in a way that could be detected by the observers, then they were mostly wagging their tails. This suggests that tail wagging was a neutral tail posture, thus it was exhibited when no social stimulus was present (HAUSFATER 1977). However, tail wagging is presumably used by herbivores to repel biting insects. The impact of biting insects on the behaviour of wood bison can be substantial (MELTON *et al.* 1989). We did not observe wood bison during insect free seasons. It is conceivable, that bison do not wag tail during the winter. If true, we suspect that they keep their tails down as a neutral position.

Tail horizontal and up was associated with aggression, sexual behaviour, and danger. Thus, the same tail posture was associated with different behaviours in different contexts. This could potentially make the interpretation of tail postures difficult. We point out, however, that when recording tail postures of bison, it is important to know the behavioural context and the sex of the animal. We feel that this requirement is easily met by an observer, because the behaviour for each animal under observation and that of the surrounding animals is usually known for a period of at least a few seconds.

The above consideration is further illustrated by tail postures not examined in our study. For example, cows can exhibit tail horizontal or tail up after copulation. The tail posture of cows in such a situation may last for one to several hours (McHUGH 1958; HERRIG and HAUGEN 1969; BERGER 1989). Tail up is also exhibited during defecation (HERRIG and HAUGEN 1969). The contexts of such tail postures are unmistakable.

We agree with McHUGH (1958) and ROTHSTEIN and GRISWOLD (1991) that discriminating between playful and agonistic interactions in the wild is often difficult without relying on subjective interpretation. Our results suggest that bison did not raise their tail in a playful context, while they did so at the end of aggressive interactions. Moreover, the intensity of an interaction seemed to be indicated by the height to which the tail was raised.

Tail up in the alert context seemed to be associated with irritation (McHUGH 1958). While we presented data on bison reacting to human disturbance, we also observed that bison reacted similarly to the disturbance by wolves.

Results presented in this study support the concept that the tail in bison may be employed in visual communication. We do not claim, however, that the evidence is conclusive. A rigorous investigation of behavioural relationships among bison receiving a signal and bison sending a signal is required. Our results suggest that tail postures of bison can serve as an objective tool in the interpretation of bison social behaviour. In fact, in many studies describing social behaviour of animals and the corresponding body postures, the tail was part of the description (SCHENKEL 1947; LEYHAUSEN 1956; WALTHER 1958; JARMAN 1979; BARRETTE 1977; CARO 1986). Conceivably, the tail could be used in species other than bison as an easily observable, objective tool to describe and interpret behaviour.

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